Copeia, 1984(3), pp. 662–671

Footprints of the Komodo Monitor and the Trackways of Fossil Reptiles

KEVIN PADIAN AND PAUL E. OLSEN

Footprints taken experimentally of a captive Komodo monitor (*Varanus komodoensis*) were recorded in potter's clay and cast in plaster. These show morphologic features, also seen in fossil footprints of large reptiles, that reflect a particular pattern of stance and gait. Footprint form and kinematics must be analyzed separately for fore- and hindlimbs because a certain amount of mosaic evolution occurs in limb morphology and locomotion. Comparisons of footprint form with still photographs of the animal walking reveal that the distinct, unmuddied prints of the manus result from an effectively parasagittal movement of the forearm and hand, rotating around a horizontally-oriented humerus. This differs from the lateral arc of protraction in the forearm movement of crocodiles, whose manus prints are generally less distinct. The monitor's pes moves parasagittally, somewhat as in crocodiles. Tail marks were not conspicuous.

The Komodo monitor tracks are similar in great detail to those of Triassic pseudosuchian thecodonts and (to a lesser extent) Early Jurassic crocodiles. Footprint faunas since the Upper Triassic are completely devoid of similar tracks. The similarities probably reflect retention in all these groups of a primitive reptilian locomotory pattern. Hence, the Komodo monitor tracks underscore the extent to which fossil footprints are classified by grade of organization and locomotion. Lacertilian tracks are uncommon in the fossil record. Similarities of Komodo monitor tracks to fossil footprints of nonlacertilians suggest that analysis of modern lacertilian footprints may provide insight into ontogenetic and functional differences underlying much of the basis of paleoichnologic taxonomy.

FOSSIL footprints have been a valuable source of data to vertebrate paleontologists for nearly two centuries. Footprints often occur in environments of deposition in which bones, the principal source of paleovertebrate data, are rare or absent. They can be used to identify the presence of certain taxonomic groups in otherwise fossil-barren sediments, and to assist in biostratigraphic correlation of other such sediments containing osteological or ichnologic remains (Olsen and Galton, 1977; Olsen, 1980a, b). However, apart from such stratigraphic associations and some rudimentary identification of certain footprint forms with presumed trackmakers, there is as yet no cohesive approach to the study of vertebrate ichnology. Our goal in this and other papers is to compare trackways of fossil and recent reptiles with respect to 1) taxonomy, 2) functional determinants of footprint form and 3) the effects of substrate conditions on trackway form and preservation. Trackmaking processes and patterns of modern animals can shed light on the functional determinants of form in fossil footprints, as well as on the locomotory patterns of the animals that made them.

Interpretation of the trackmakers that left fossil footprints dates back to the early 19th Century, when such tracks were first treated in a scientific context. Early workers (Hitchcock, 1848; Deane, 1861) pressed the feet of stuffed or preserved reptiles into clay molds in an attempt to simulate footprints, but this technique ignored kinematics of the step cycle and its effects on footprint form. Later workers examined tracks of modern reptiles in zoos (von Huene, 1913) or occasionally in the wild (Reineck and Howard, 1978), but few systematic functional analyses of these tracks were made (Rühle von Lilienstern, 1939). Schaeffer (1941) studied the footprints of a small caiman on smoked glass, and Peabody (1948) examined those of salamanders on smoked paper, but neither medium is a good analogue for a natural substrate, and so the animal's normal gait and footprint morphology were both abnormally altered. Footfall patterns of modern animals have been taken in conjunction with studies of locomotion (Gambaryan, 1974), but the use of footprints in this context has focused less on morphologic and kinematic details of the pedes, and more on specific types of gaits and the speeds associated with them. Some of these studies have been extended to fossil trackways (Alexander, 1976; Farlow, 1981).

We wish to stress here the process of trackmaking as it applies to the anatomy of the animal and the condition of the substrate. Baird (1957) emphasized that a footprint is not a static record of morphology, but a dynamic record of an animal in contact with a particular substrate under particular environmental conditions. We find it useful to separate three influences contributing to trackmaking: the anatomy of the foot, the kinematics of the step cycle, and the nature of the substrate (Padian and Olsen, in press). The interrelationships of these variables are not well understood in the footprints of modern animals, a problem that contributes to the difficulties of fossil footprint taxonomy. Therefore, a great deal can be learned from experimental studies of the footprints of modern reptiles.

The purpose of this work is to describe footprints of the Komodo monitor (*Varanus komodoensis*) that were produced experimentally in order to compare footprint morphology with foot anatomy and kinematics of the step cycle, and to compare details of these tracks with those of fossil footprints. We hope to point out the potential value of footprints to the study of stance and gait in both modern and extinct reptiles, and to emphasize the distinction between foot form and footprint form that must be taken into account in the classification of fossil footprints. We chose the Komodo monitor for study in this context because it is the largest fully terrestrial reptile, and is regarded as a relatively primitive member of a conservative group of lizards with a long geological history (Auffenberg, 1981:45). Because its behavioral ecology and anatomy are reasonably well known, details of its footprints and the process of trackmaking can be related directly to other aspects of its biology.

MATERIALS AND METHODS

With the cooperation of the research branch of the San Diego Zoological Society, we used two Komodo monitors at the San Diego Zoo. These are a large male (SDZ 1131) and a smaller female (SDZ 0305). The male was born of wild-caught parents at the Jogjakarta Zoo on 1 June 1958; at three months of age he was brought to Basel, where he lived until coming to the San Diego Zoo in 1976. At the time of this study (August 1981), he was just over 13 years old. The female arrived at the San Diego Zoo in 1967; Zoo records indicate that she was already "four feet" long. Her age is unknown. Shortly after arriving at the Zoo she sustained injuries from a fall, and her growth rate appears to have slowed considerably from that point on, according to Curator James P. Bacon. We note these facts because, for reasons related to their lives in captivity, certain biologic measurements and data may be atypical of feral Komodo monitors, and we urge caution in interpreting our results too broadly. The female is blinded by cataracts and has an erratic gait; because of her disability we did not use her in the trackmaking study. We did photograph and analyze the soles of her feet to compare with the trackway of the male, who is difficult to handle. The female is nearly 1.8 m in total length and weighs about 26.25 kg (data taken 8 Jan. 1981). The male is 2.54 m and weighs 82.5 kg; his girth, measured just behind the shoulder, is 94 cm (data taken 9 May 1981). Their weights are nearly twice the norms reported for feral monitors, due to their largely sedentary life in captivity (Auffenberg, 1981:27).

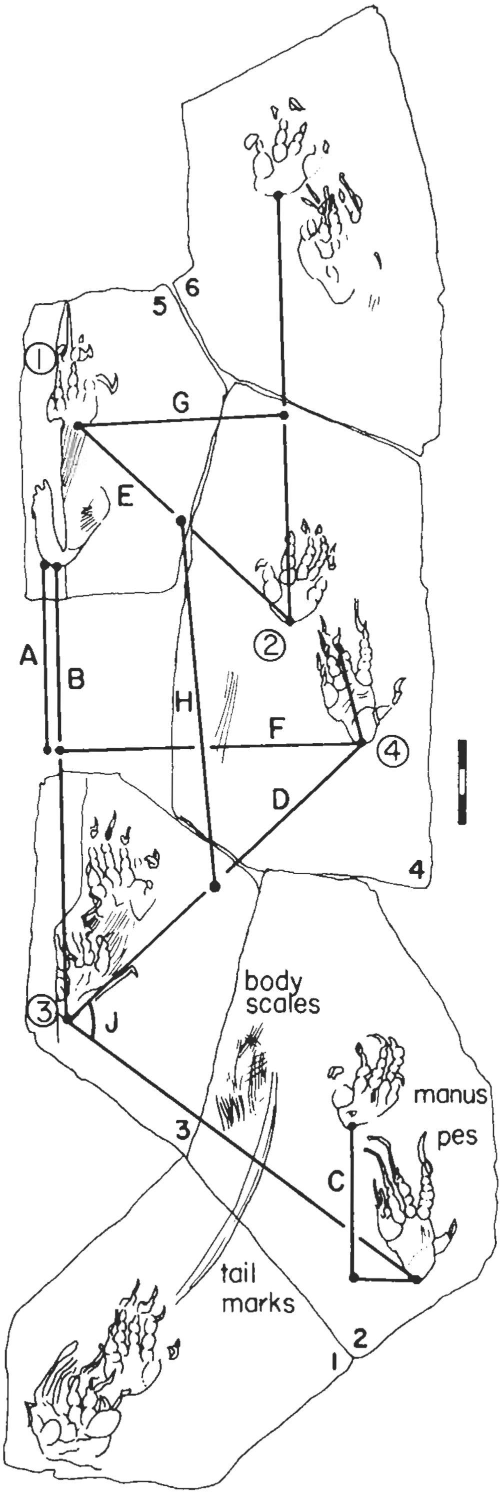
The Komodo monitor enclosure at the Zoo can be partitioned into two halves by a sliding door. While the male was enclosed in one half we prepared a trackbed of moist, fine potter's clay just outside the connecting door. The trackbed was mixed so as to simulate a firm substrate, cut into slabs 2.5 cm thick, and laid on a bed of plywood sheeting 91 cm wide and 244 cm long. No other preparation of the substrate was necessary, but occasionally we sprayed the surface with water to replenish evaporated moisture.

The male was lured across the clay trackbed by the attraction of a freshly killed rat suspended from a pole held by one of the keepers. He walked normally and was allowed to seize the bait after successfully negotiating the trackbed. [This took two attempts; details of the procedure and additional photographs are given in Padian (1981)]. When the male was enclosed once again on the other side of the cage, we took molds of the trackbed in plaster of Paris for better preservation and ease of handling. Before molding, the trackbed was divided into six parts by cardboard; the plaster was reinforced internally with chicken wire and marked for reassembly when dry. Each part contains one manus-pes set of footprints.

Results

Measurements.—The reconstructed trackway is illustrated in Fig. 1; the principal measurements are given in Table 1. All analyses of the trackway were carried out on the plaster molds, which differ from the clay trackbed because they 1) produce a "positive" bas-relief impression of the "negative" clay trackbed, and 2) cause the left side to be positioned on the right, and vice versa. To avoid confusion we will refer here to the "right" foot as that positive impression which appears on the right side of the plaster mold, even though this is actually a mold of the left footprint.

The footprints of the right side were quite clear and well detailed; those of the left side were not as clear because the monitor planted his feet directly on the edge of the clay. A representative set of manus and pes prints is illustrated in Fig. 2. The manus print is about 19 cm long and is slightly medial and anterior to the pes print, which is about 22 cm long (both measured from the base of the heel to the tip of digit IV, the longest in both manus and pes). On average, the posterior border of the manus print was situated approximately 22 cm anterior and 12 cm medial to the posterior border of the pes print. The distance between successive prints of the same foot ranged from 80 to 100 cm (mean = 91). The manus prints occur at an average distance of 20 cm from the midline of the body, the pes prints at 30 cm from the midline. Digit IV of the pes points approximately in the direction of travel: the first three digits are toed-in at an angle of about 15°, and the fifth digit is toed-out at about 35°. In the manus, digit I is toed-in at about 15°, and digits II–V are toed-out at about 20°, relative to the direction of travel (digit II a bit less than the others). Digit III is only slightly shorter than digit IV in both manus and pes.



←

Fig. 1. Trackway of *Varanus komodoensis* (UCMP 127161), drawn from plaster molds. Measurements given in Table 1. Scale bar divisions = 5 cm. Circled numbers (1–4) represent position of feet during measurement of mid-glenoid length (E), mid-acetabular length (D) and gleno-acetabular length (H).

TABLE 1. MEASUREMENTS OF *Varanus komodoensis* TRACKWAY (UCMP 127161).

Datum	Measurements	Mean
A. Pace length	35, 48, 51, 41, 54, 56, 37, 40	45
B. Stride length	85+, 90, 100, 94, 90, 92, 80, 80	89
C. Distance between bases of ipselateral manus and pes pairs	22+, 30, 18, 22, 21, 22	23
D. Distance between consecutive prints of left and right pes	75, 83, 76, 69, 73	75
E. Distance between consecutive prints of left and right manus	65, 57, 64, 54, 58	60
F. Distance between left and right pedal trackways	65, 62, 57, 54	60
G. Distance between left and right manual trackways	42, 40, 36, 43	40
H. Gleno-acetabular length	67, 69, 69, 62.5	67
I. Length of digits, measured from posterior portion of footprint (heel)		
Manus	I	13
	II	17
	III	19
	IV	19
	V	15
Pes	I	16
	II	20
	III	21
	IV	22
	V	12.5
J. Pace angulation	73°, 80°, 78°, 73°	76°

Notes: All measurements in cm except when indicated. A and B are calculated for both manus and pes. I is based on measurements from panels 2 and 4, Fig. 1. J is the angle measured between the bases of the third pedal digits of three consecutive footfalls.

Based on the mold of the trackway (Fig. 2A), an outline of the interphalangeal pads was made (Fig. 2B) and the bony structure restored (Fig. 2C). The restoration agrees with the phalangeal formula and proportions of the Komodo monitor (2-3-4-5-3 in the manus and 2-3-4-5-4 in the pes), because the precise placement of the feet during the monitor's step cycle results in little distortion of foot anatomy in the footprint.

Estimates of gleno-acetabular length were taken following Baird's (1952, 1954, 1957) method for fossil footprints. Assuming that all four feet are implanted on the ground at once, if only briefly, the mid-acetabular point may be estimated by measuring the distance halfway between left and right tarsi (Fig. 1:D), and the mid-glenoid point by measuring the distance halfway between left and right carpi (Fig. 1:E). The gleno-acetabular length is estimated by measuring the distance between these midpoints (Fig. 1:H). Each step permits another estimate of gleno-acetabular length. The values obtained in this way were 67, 69, 69, and 62.5 cm (mean = 67 ± 3.1). The last corresponds to a point in the trackway where the animal took a significantly shorter step (80 cm in both manus and pes) than in the remaining trackway (range = 90–100 cm). On 26 October 1982, sometime after this work was completed, Keeper Susan Schafer was able to take a reading of the animal's gleno-acetabular length during a torpid period early in the morning. Her estimate of 71 cm accords well with our estimate of 65 to 75 cm, based on photographs, and with the estimates from trackways listed above.

Stance and gait.—Observations of the kinematics of the step cycle revealed that there is almost no rotation of the foot in leaving the ground (Fig. 3). The extreme clarity of the prints reflects a precise, almost deliberate implantation of the feet on the substrate. In the Komodo

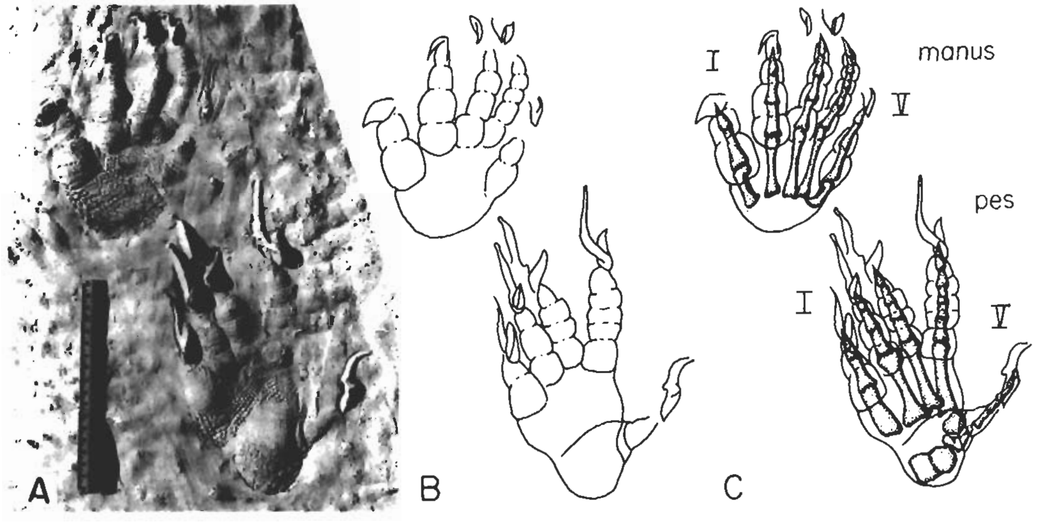


Fig. 2. Mold of one manus-pes set of footprints from UCMP 127161. A) photograph of plaster mold (scale in cm); B) reconstruction of the same as preserved; C) restoration of the bones of the foot in its print. For explanation see text.

monitor the humerus appears to be maintained in a more or less horizontal, lateral position with relatively little protraction and retraction; instead, rotation at the shoulder and wrist appears to account for most of the motion of the forelimb (Fig. 3). This results in a more parasagittal motion of the forefoot, with little or no lateral arc. The morphology of the track therefore corresponds closely to the morphology of the foot.

The great detail of these footprints is due both to the animal's plantar step and the competence of the substrate. Scale impressions are quite distinct except in the metatarsal region, where the skin is looser than on the digits and over the ankle. Some sliding took place when the animal moved out of the track, as the very long anterior trails of the unguals suggest. The claw marks show two main features: a deep proximal depression made during the initial transmission of force through the foot to the substrate as the foot lands, and a progressively shallower anterior trail made as the foot moved forward again, dragging slightly in the process. These features are particularly distinct because the claws of these captive animals are so long, a result of relative inactivity and lack of wear: in the wild the claws of *V. komodoensis* are relatively shorter than in other varanids (Auffenberg, 1981:26).

Generally speaking, the deepest impressions were left in areas where the scale patterns on the foot showed the most wear. These were primarily on the interphalangeal areas of the pads of fore- and hindfeet, and on the tarsometatarsal joint. The shallowest impressions were made in the metacarpal and carpal regions. In both manus and pes, impressions of digits I–III were the deepest, and IV–V the shallowest, as would be expected from the vectors of transmission of the body weight.

Impressions of body scales appear in several places where the animal alit or brushed the ground. Only one light impression of the tail is evident on the 2.6 m trackway: it is 2 cm wide and 56 cm long (Fig. 1).

DISCUSSION

Analysis of Komodo monitor footprints.—In a previous study comparing the tracks of recent and fossil reptiles (Padian and Olsen, in press), we analyzed the tracks of a small caiman (*Caiman sclerops*) under controlled conditions similar to those used here. Several comparative features of caiman and Komodo monitor tracks are instructive in the interpretation of fossil footprints.

Despite detailed differences in the structure of the pedes and the musculature of the hindlimbs, the tracks of the hindfoot of the caiman and Komodo monitor are both very distinct: there are good impressions of nearly all pha-

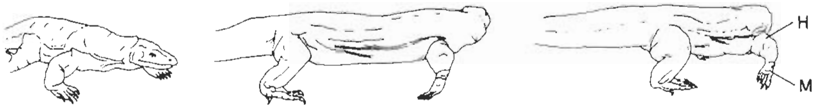


Fig. 3. Line drawings of three still photographs of *Varanus komodoensis* (SDZ 1131), showing orientation of limbs when walking. Notice especially in the third frame the horizontal position of the humerus (H) and the nearly parasagittal position of the manus (M). Length of pes approximately 22 cm.

langes and very little muddying of the print takes place. This superficial similarity is due to the very stable contact of the foot on the substrate in both animals. The implantation of the foot, as noted above, is suggestive of a precise, deliberate gait in which most of the movement of the foot is parasagittal. However, these gaits differ in the Komodo monitor and the caiman. In the "high walk" of the caiman, the femur is directed anteroventrally and laterally at the beginning of the propulsive phase, and abduction of the femur in the step cycle is about 20° (Brinkman, 1980). The tibia and fibula rotate during plantarflexion but move in an essentially parasagittal plane, while the foot is turned out during lateral rotation of the tarsus. This rotation of the foot is initiated as the animal leaves the substrate, and the effect on footprint form is negligible. In the sprawling step cycle of the caiman, abduction of the femur is about 50° (Brinkman, 1980). This greater degree of abduction in sprawling corresponds more closely to the step cycle we observed in the Komodo monitor, in which considerable excursion of the femur occurs. However, analysis of still photographs taken during the step cycle of the Komodo monitor suggests that the degree of rotation of the tarsus is comparable to that of the caiman, resulting in relatively distinct tracks. This suggests that movement at the tarsus may be the primary determinant of clarity in footprint form.

In contrast, the forelimb step cycles of the caiman and Komodo monitor are quite different, and these differences are manifested in their footprints. In the caiman, there is considerable lateral excursion of the humerus and forearm; the forefoot swings laterally into the footprint, dragging the digits as it lands (Padian and Olsen, in press). The manus print points anterolaterally with digit III oriented 45°–90° lateral to the direction of the animal's progress. As a result of this dragging, the positions of the juvenile caiman's digits are highly variable, and frequently certain digits make no impression at all. The caiman's manus prints are relatively sloppy, indistinct, and quite variable. This is not the case with the Komodo monitor, whose prints appear to be much more consistent in form. In crocodiles the forelimb is extended laterally so that the elbow is flexed while the humerus is protracted, resulting in a lateral arc of the forefoot. But in the Komodo monitor the humerus is held laterally with relatively little protraction and retraction; instead, rotation of the humerus through an arc of about 70° accounts for the principal movement. As a result, the forearm and manus move in a parasagittal plane, and there is relatively little rotation at the wrist. The manus prints of the Komodo monitor are therefore unmuddied by the kinematics of the forelimb.

Overstepping (in which the print of the hindfoot is laid down in front of the immediately preceding print of the ipselateral forefoot) occurs in reptiles when the dorsal vertebral column is short or the hindlimbs are considerably longer than the forelimbs (or both). High lateral flexure of the vertebral column may contribute to this (D. Baird, pers. comm.). At increased speeds overstepping may be exaggerated, and shifting to bipedalism (as some lizards do) is one solution to this problem. The trackway we took of the Komodo monitor shows no overstepping. Auffenberg (1981:26) observed that the hind limbs are relatively short and stout in adult Komodo monitors, and large in juveniles. We predict that in juveniles the spatial relationship of manus and pes prints differs from that of adults, as it appears to do in some fossil footprint forms (Haubold, 1971) and in crocodiles. Therefore, although the pes of this adult did not overstep the manus in our experiment, it does not preclude the possibility of doing so under other circumstances. Juvenile Komodo monitors may overstep frequently or habitually, and it would be instructive to compare ontogenetic series of related taxa to examine phylogenetic patterns of growth and gait change.

The comparison between caiman and Komodo monitor footprints becomes most instructive in turning to the fossil record of reptilian footprints. Despite anatomical and functional differences between the caiman and Komodo monitor, their footprints are somewhat similar. This fact becomes important in the interpretation of morphology, taxonomy, and locomotion of extinct forms. One of the principal goals of our study was to compare footprints of a large modern reptile, recorded under known conditions, with those preserved in the fossil record. The prints of the Komodo monitor taken in our study show some strong similarities to a group of fossil footprint form genera common in the Triassic and Early Jurassic, but not recorded since that time (200 mybp). However, this observation needs to be set in context. Meaningful comparisons cannot be made without an appreciation of the taxonomy of footprints, and of the temporal and stratigraphic biases that contribute to the record of fossil footprints.

Paleoichnologic taxonomy.—Footprints, like other trace fossils, are form taxa that represent biologic processes, not biologic structures. Since the 19th Century, footprints have been classified on the basis of their general shape, size and details of their form. Baird (1957) stressed that "typological analysis of isolated examples cannot be expected to yield zoologically significant information," and urged taxonomists to consider primarily those characters that reflect the bony structure of the foot, not simply those that describe the shape of the footprint. But this goal is not easily met. By their nature, footprints reflect a grade of functional organization difficult to separate from characters useful for taxonomic identification on other grounds. One present difficulty is that the characters of the hindfoot alone usually determined general systematic placement of the trackway (Demathieu 1970:19). This is unfortunate because the morphology and step cycle of the hind feet are often quite generalized and may retain many primitive characters. Form genera with similar pes prints may accompany manus prints that are often quite different from each other, and contain data that exclude some systematic assignments, while suggesting others (e.g., the Jurassic trackway *Pteraichnus,* originally assigned to a pterosaur but reinterpreted as crocodilian by Padian and Olsen, in press). The analysis of Komodo monitor prints indicates that taxonomy based solely on the pes may mask important phylogenetic distinctions revealed by the manus.

Systematic analysis of Komodo monitor footprints.—The Late Triassic and Early Jurassic periods witnessed a dramatic faunal turnover in the reptilian realm that ushered in the replacement of the more archaic thecodonts and other forms by dinosaurs and crocodiles. The abundant footprint taxa of these times were grouped by Nopcsa (1923) into several categories, revised by Lull (1953), Baird (1954, 1957), Demathieu (1970), Haubold (1971) and others. The five major divisions commonly recognized, and their probable trackmakers, are "stegocephaloids and salamandroids" (large and small amphibians), "lacertoids" (most early and many later reptiles of generalized gait), "crocodiloids" (crocodiles, thecodonts of various types, some dinosaurs, and some non-archosaurs), "dinosauroids" (tridactyl prints of theropod and ornithopod dinosaurs) and "theromorphoids" (mammal-like reptiles and other forms that produced an aggregate of variable tracks not belonging clearly to any other division). Among these, the footprints of the Komodo monitor show diagnostic similarities to the crocodiloid group. In this group [following the criteria of Nopcsa (1923)], the third digit of the pes is elongated and the toes directed forward. *Batrachopus* (Fig. 4A) has a functionally four-toed foot with the third toe the longest; this footprint genus, from the Early Jurassic of the Connecticut Valley, was referred to the contemporaneous skeleton of *Stegomosuchus* by Lull (1915), and is now recognized as a crocodile trackway (Haubold, 1971). *Chirotherium* (Fig. 4B) is a well-known Triassic footprint form belonging to this group (Soergel, 1925; Baird, 1954), distinguished by a long third digit and a small fifth digit that turns outward and backward. The trackmaker is usually inferred to have been a pseudosuchian thecodont. *Apatopus* (Fig. 4C) was identified as the track of a phytosaur by Baird (1957), who noted the aquatic features of a pes with non-crocodiloid structure. The fourth digit is secondarily elongated, even though the fourth metatarsal retains the primitive condition of being shorter than the third, as in the Komodo monitor. The "pseudosuchian" assignment for *Chirotherium* also applies to the quite similar footprint *Synaptichnium* (Nopcsa, 1923), in which the fourth digit of the pes is the longest; the first four digits are gathered together and nearly parallel, with the fifth separate from the first four, projecting straight laterally (Fig. 4D).

In Fig. 4 these four footprint taxa are compared to line drawings of the Komodo monitor tracks (Fig. 4E). The diagnostic characters of

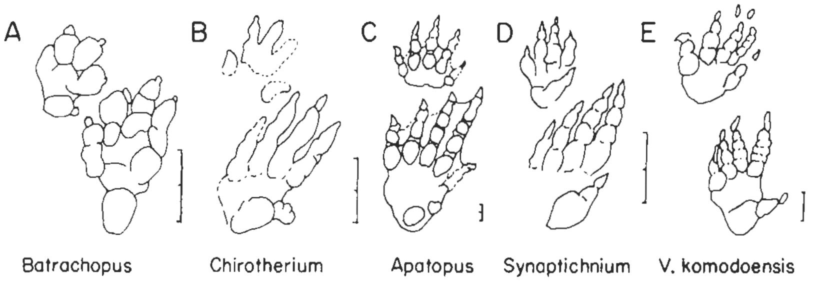


Fig. 4. Right manus and pes prints of: A) *Batrachopus deweyi,* composite of type specimen of type species (Early Jurassic, Amherst College 26/6); B) *Chirotherium lulli* (Upper Triassic, after Baird, 1954); C) *Apatopus lineatus* (Upper Triassic, after Baird, 1957); D) *Synaptichnium pseudosuchoides* (Upper Triassic, after Baird, 1954); and E) *Varanus komodoensis* (UCMP 127161, taken from SDZ 1131, composite of all tracks). Presumed trackmaker of A is a crocodile; of B and D, pseudosuchian thecodonts; of C, a phytosaur. In A, not all digits are represented (this is typical of crocodile tracks). Manus and pes are oriented with respect to direction of travel (indicated by scale bars), although the distance between manus and pes is variable and should not be taken literally. Scale bars = 2 cm, except in E, 5 cm. Tracks are arranged in order of increasing similarity to those of *V. komodoensis.*

Synaptichnium and *Apatopus* listed above are partly suggested in the varanid footprints. However, the latter has several unique features pertaining to the orientation of the pes, the relatively large manus and its phalangeal formula, and the divarication of the digits. The features it shares with the "crocodiloid" footprint group of Nopcsa are either plesiomorphic characters of foot form and locomotion, or are merely resemblances acquired convergently (e.g., the divergent fifth toe).

There are almost no good herpetological ichnofaunas after the Late Triassic that are not dominated by the very specialized trackways of dinosaurs. Dinosaurian footprints provide little clue to the animals that made the non-crocodilian "crocodiloid" tracks discussed above. Perhaps because the environments in which they live are not amenable to geologic preservation, we have no good footprint records of lizards and other lepidosaurs unless *Rhynchosauroides* is a lepidosaur track [Olsen (1980b) for another possible example see Haubold (1971:52)], but these are not similar to the *V. komodoensis* tracks. Consequently, the "best fit" for Komodo monitor tracks among those preserved in the fossil record is not particularly appropriate in terms of phylogeny or morphology. The accident of sampling in the preserved paleontologic record is such that we know less about the fossil trackways of extant groups than about those of extinct ones. For many otherwise well-known fossil groups (e.g., turtles, lizards, pterosaurs, frogs, and several kinds of dinosaurs including stegosaurs, ankylosaurs and ceratopsians) there are no known footprint records, or at best only a few.

Form and function in "crocodiloid" footprints.—The inferred trackmakers of the "crocodiloid" footprint group, though phylogenetically and morphologically diverse, are nonetheless all non-dinosaurian archosaurs—that is, "thecodonts" and crocodiles, the locomotion of the latter being considered more or less functionally equivalent to a "thecodont" grade of locomotion (Charig, 1972). The striking similarities of such tracks to those of a modern-day giant lizard (that is not a typical "sprawler") suggest strongly that a functional grade of organization, not necessarily a phylogenetic pattern, is reflected by this group of footprints. Differences in detail among such footprint taxa may be functionally insignificant and anatomically subtle; however, the differences may be phylogenetically misleading because a primitive or convergent mode of locomotion is being employed. Phylogenetic differences may be swamped by overall similarity of locomotor pattern. It may be important that the fifth digit is very reduced (as in crocodiloids and the referred tracks *Batrachopus* and *Otozoum*) or is rectilinear and divergent outward (as in the Komodo monitor and *Synaptichnium*: perhaps the latter feature is a clue to juvenile arboreality, as in many lizards including *V. komodoensis*). As Baird (1957) suggested, ichnologic features reflecting diagnostic osteologic characters must be identified in order for their taxonomy to be comparable to morphologic taxonomy. The search for shared derived characters in footprint form-taxa may then allow locomotory evolution to be read from the functional analysis of footprints.

We wish to stress that the overall similarity of the Komodo monitor tracks to the footprint taxa discussed above should not lead to the inference that Komodo monitors or their immediate relatives have existed since the Triassic, even though other lines of fossil evidence suggest an early origin for lizards (Carroll, 1977; Evans, 1980). We think it likely that the general locomotory pattern responsible for the footprint morphology obtained here is ancient and may have been derived independently in several reptilian groups. In orientation, though not in proportions, the "crocodiloid" footprint group, which contains mostly thecodont tracks, retains a basic locomotory pattern seen in "lacertoid" and "stegocephaloid" taxa since the Paleozoic (Haubold, 1971). Other groups of Mesozoic reptiles show various modifications of this pattern. In true crocodiles the fifth pedal digit is greatly reduced, and they walk with the manus turned outward. Several groups of dinosaurs became bipedal, reduced the outer toes, and walked parasagittally, or grew so large that their stance and gait became elephantine. Other well-known modifications of stance and gait evolved independently in therapsids and mammals. Therefore the grade of locomotory evolution in thecodonts, apparently attained also in the Komodo monitor, is certainly paraphyletic and may be polyphyletic as an evolutionary pattern. Only a full study of comparative locomotory and ichnologic patterns in a variety of fossil and modern forms will shed further light on this question.

CONCLUSIONS

In 1859 Thomas H. Huxley remarked, "It must be confessed that there is a great want of recent materials in attempting to study comparative ichnology." Fossil footprints comprise a great deal of the available fossil record of lower vertebrates, especially in many Mesozoic and Late Paleozoic sediments. Interpretations of these trackways have been hampered by inadequate understanding of the process of trackmaking. The anatomy of the foot, the kinematics of the step cycle, and the competance of the substrate must all be considered (Padian and Olsen, in press). The study of recent animals, though still not pursued systematically, is the best hope of overcoming deficiencies in our understanding of paleoichnology.

The footprints of the Komodo monitor demonstrate the degree to which superficial similarities in footprint forms may mask extensive differences in locomotion and systematic membership of the trackmakers. Although the Komodo monitor's footprints bear strong resemblance to certain "crocodiloid" fossil trackways—and indeed would probably have been classified among this group if the true identity of the trackmaker were unknown—most of this resemblance is convergent. All indications are that the "crocodiloid" footprint group of the Early Mesozoic is composed of archosaurs of thecodontian grade, not of lepidosaurs. Because the taxonomic treatment of the fossil footprints has been based on the overall shape of the hindfoot, important differences in the forefoot, often reflecting possible facutative bipedality or a history of bipedality, have tended to be ignored. The taxonomic treatment of fossil footprints is wholly divorced from that of their trackmakers, as befits form taxa. What Demathieu (1970) has called the "parataxonomy" of footprints can be made biologically meaningful by full analysis of the data inherent in footprints. The footprints of the Komodo monitor suggest that the current basis of paleoichnologic taxonomy requires revision to include the role of the forefoot as well as an appreciation of the role of limb kinematics in the production of apparently similar trackways.

ACKNOWLEDGMENTS

We wish to thank the San Diego Zoological Society and the staff of the San Diego Zoo for their cooperation and kind permission to use their Komodo monitors. Special thanks go to Kurt Benirschke, Director of Research; James P. Bacon, Curator of Reptiles and Amphibians; and Keepers Tom Schultz, Robin Greenlee, Susan Schafer and Debra Dumas. We are grateful to Michael Novacek and Vera Novacek for technical assistance and hospitality, and to Donald Baird for reviewing the manuscript and offering good advice. This work was supported by a University of California Faculty Research Grant to K.P., by the Museum of Paleontology of the University of California and by NSF grant DEB 77-08412 to K. S. Thomson in support of P.O.

LITERATURE CITED

ALEXANDER, R. MCNEILL. 1976. Estimates of speeds of dinosaurs. Nature 261:129–130.

AUFFENBERG, W. 1981. The behavioral ecology of the Komodo monitor. University Presses of Florida, Gainesville.

BAIRD, D. 1952. Revision of the Pennsylvanian and Permian footprints *Limnopus, Allopus,* and *Baropus.* J. Paleont. 76:832–840.

———. 1954. *Chirotherium lulli,* a pseudosuchian reptile from New Jersey. Bull. Mus. Comp. Zool., Harvard Univ. 111:165–192.

———. 1957. Triassic reptile footprint faunules from Milford, New Jersey. *Ibid.* 117:449–520.

BRINKMAN, D. 1980. The hind limb step cycle of *Caiman sclerops* and the mechanics of the crocodile tarsus and metatarsus. Canad. J. Zool. 58:2187–2200.

CARROLL, R. L. 1977. The origin of lizards. Linn. Soc. Symp. Ser. 4:359–396.

CHARIG, A. J. 1972. The evolution of the archosaur pelvis and hindlimb: an explanation in functional terms, p. 121–155. *In:* Studies in vertebrate evolution. K. A. Joysey and T. S. Kemp (eds.). Oliver and Boyd, Edinburgh.

DEANE, J. 1861. Ichnographs from the sandstones of Connecticut River. Little, Brown, and Co., Boston.

DEMATHIEU, G. 1970. Les empreintes de pas de vertébrés du Trias de la bordure nord-est du Massif Central. Cahiers de Paléo., Ed. CNRS, Paris.

EVANS, S. E. 1980. The skull of a new eosuchian reptile from the Lower Jurassic of South Wales. Zool. J. Linn. Soc. 70:203–264.

FARLOW, J. A. 1981. Estimates of dinosaur speeds from a new trackway site in Texas. Nature 294: 747–748.

GAMBARYAN, P. P. 1974. How mammals run. Halsted Press, New York.

HAUBOLD, H. 1971. Ichnia Amphibiorum et Reptiliorum fossilium. Handbuch der Paläoherpetologie, Teil 6. Gustav Fischer Verlag, Stuttgart.

HITCHCOCK, E. 1848. An attempt to discriminate and describe the animals that made the fossil footmarks of the United States, and especially of New England. Mem. Amer. Acad. Arts Sci. NS 3:129–256.

HUENE, F. VON. 1913. Beobachtungen über die Bewegungsart der Extremitäten bei Krokodilen. Biol. Cent. 33:468–472.

HUXLEY, T. H. 1859. On the *Stagonolepis robertsoni* (Agassiz) of the Elgin Sandstones; and on the recently discovered footmarks in the sandstones of Cummingstone. Quart. J. Geol. Soc. Lon. 15:440–460.

LULL, R. S. 1915. Triassic life of the Connecticut Valley. Conn. State Geol. and Nat. Hist. Surv. Bull. 24.

———. 1953. Triassic life of the Connecticut Valley, revised. *Ibid.* 81.

NOPSCA, F. 1923. Die Familien der Reptilien. Fort. Geol. Palaeont. 2.

OLSEN, P. E. 1980a. A comparison of the vertebrate assemblages from the Newark and Hartford basins (Early Mesozoic, Newark Supergroup) of eastern North America, p. 35–53. *In:* Aspects of vertebrate history. L. L. Jacobs (ed.). Mus. N. Ariz. Press, Flagstaff.

———. 1980b. Fossil great lakes of the Newark Supergroup, p. 352–398. *In:* Field studies of New Jersey geology and guide to field trips. 52nd Ann. Mtg., New York State Geol. Assoc. W. Manspeizer (ed.). Newark College of Arts and Sciences, Newark, N.J.

———, AND P. M. GALTON. 1977. Triassic-Jurassic tetrapod extinctions: are they real? Science 197: 983–986.

PADIAN, K. 1981. Komodo dragons fit Triassic trackways. Zoonooz (San Diego Zool. Soc.) 54 (12):16–17.

———, AND P. E. OLSEN. In press. The fossil trackway *Pteraichnus*: not pterosaurian, but crocodilian. J. Paleont.

PEABODY, F. E. 1948. Reptile and amphibian trackways from the Lower Triassic Moenkopi Formation of Arizona and Utah. Univ. Calif. Publ. Geol. Sci. 27:295–568.

REINECK, H.-E., AND J. D. HOWARD. 1978. Alligatorfährten. Natur und Museum 108:10–15.

RUHLE VON LILIENSTERN, H. 1939. Fährten und Spuren im Chirotheriumsandstein von Südthüringen. Fort. Geol. Paläont. 12:293–387.

SCHAEFFER, B. 1941. The morphological and functional evolution of the tarsus in amphibians and reptiles. Bull. Amer. Mus. Nat. Hist. 78:395–472.

SOERGEL, W. 1925. Die Fährten der Chirotheria: eine paläobiologische Studie. Gustav Fischer Verlag, Jena.

DEPARTMENT OF PALEONTOLOGY, UNIVERSITY OF CALIFORNIA, BERKELEY, CALIFORNIA 94720; AND YALE PEABODY MUSEUM, PO BOX 6666, NEW HAVEN, CONNECTICUT 06511.

Accepted 23 Sept. 1983.